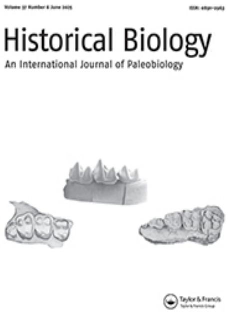

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BRIEF REPORT

Isoxys carbonelli and the palaeoenvironmental disparity of *Isoxys* during Cambrian Stage 3

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ABSTRACT
In 1927, Rudolf and Emma Richter found a unique specimen of bivalved arthropod, which they named *Isoxys carbonelli* (Richter & Richter, 1927), and accessioned at the Senckenberg Museum of Natural History of Frankfurt, Germany. Since then, the specimen has been neither redescribed nor re-illustrated. A century later, we redescribe and re-illustrate the holotype and only specimen of *I. carbonelli* and describe the geological setting with reference to a modern biostratigraphical framework. In addition, we compare *I. carbonelli* with other *Isoxys* species and sunnelids (another group of small Cambrian bivalved arthropods) by means of elliptical Fourier analysis and hierarchical cluster analysis. The analysis concludes that *I. carbonelli* is a valid species, one of the oldest representatives (together with *I. zhurensis* Ivantsov, 1990 from Siberia). If the specimen is an adult, *I. carbonelli* was the smallest member of the genus. *Isoxys* was widespread during Cambrian Stage 3, showing high morphological disparity and size variation. The oldest species lived in warm, shallow marine, carbonate environments alongside archaeocyaths, in the bigotonid trilobite province.

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Arthropod; Córdoba; Iberia; outline analysis; Ovetian

Introduction

Isoxys carbonelli Richter & Richter, 1927 represents one of the most unusual findings from the early Cambrian of the Iberian Peninsula. Recovered almost a century ago (Richter & Richter, 1927), this species is known from a single bivalved carapace. In their original study, Richter & Richter compared their new species to *I. chilhoweanus* Walcott, 1890 and *I. acutangulus* Walcott, 1908, united by morphological similarities such as the asymmetrical carapace with anterior and posterior spines. Although line drawings have been presented (García-Bellido, Paterson, et al., 2009; Williams et al., 1996), *Isoxys carbonelli* has not been refigured in the last 100 years, nor has its systematic position as an isoxyiid been considered in light of the much higher disparity and diversity of small Cambrian bivalved arthropod groups now known, including bradoriids and sunellids (e.g. Chen et al., 2025; Cox & Pates, 2024; Williams et al., 2007).

In the nearly 100 years since this discovery, our appreciation of the diversity and morphological disparity of small bivalved arthropods has greatly increased. Not only are many more *Isoxys* species known, with this genus now known to have had a cosmopolitan distribution albeit with provincialism at the species level (e.g. Vannier et al., 2009; Williams et al., 1996), but we also have knowledge of soft part anatomy (e.g. Zhang et al., 2023; Fu et al., 2011, 2014; García-Bellido, Vannier, et al., 2009; García-Bellido, Paterson, et al., 2009; Stein et al., 2010; Ma et al., 2023). Furthermore, the carapace shapes of *Isoxys* species have now been more comprehensively compared both qualitatively in detailed descriptions and reviews (e.g. García-Bellido, Paterson, et al., 2009; Williams et al., 1996) and quantitatively with outline analyses (Pates et al., 2021). Importantly, bradoriids, *Isoxys* Walcott, 1890 and sunellids all possess bivalved carapaces, are members of the euarthropod stem lineage, and share numerous carapace features (Zhai et al., 2019; Zhang & Shu, 2007; Zhang et al., 2023). Bradoriids are generally small (most <10 mm), *Isoxys* large (most >20 mm), and sunellids intermediate in size (6–15 mm). Anterior and posterior spines are known in both *Isoxys* and sunellids (though absent in the isoxyiid *Surusicaris* Aria et al., 2015), and absent in bradoriids (Aria et al., 2015; Chen et al., 2025; Williams

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et al., 1996, 2007). Sunellids share the presence of an anterodorsal sulcus, which is absent in *Isoxys* (X. Zhang & Shu, 2007). Because of its small size, and short spines, *I. carbonelli* shares features with sunellids and *Isoxys*. As the family Sunellidae Huo, 1965 was formalised nearly 40 years after *I. carbonelli* was described, and as sunellids are now known to have not been restricted to South China, but were present in Gondwana (Chen et al., 2025), and a species previously considered as *Isoxys* has recently been redescribed as a sunellid (Sun et al., 2021), the status of *I. carbonelli* as *Isoxys* requires re-evaluation in a modern context.

Herein, we provide the first re-illustration of the holotype of *I. carbonelli* in almost 100 years, in combination with an updated description, we evaluate whether this species is still best considered *Isoxys* or as a sunellid. To further interrogate support for *I. carbonelli* as *Isoxys* we quantify and compare carapace shapes of *Isoxys* and sunellids, using elliptical Fourier analysis and hierarchical cluster analysis. Finally, we consider the palaeoenvironmental and stratigraphical position of *I. carbonelli*.

Geological setting

The study section, historically named Las Ermitas, is located in the Sierra de Córdoba, southern Spain, belonging to the Córdoba Block of the Ossa-Morena Zone, south-western Iberian Massif (Liñán & Quesada, 1990) Figure 1(A,B). The Córdoba block is mostly composed of Cambrian rocks which follow a syncline trending NW – SE, dipping to the SE, with the northern flank interrupted by the so-called Cerro Muriano Fault and to the south by the Precambrian rocks of the San Jerónimo Formation. The Cambrian lithostratigraphy framework of the Sierra de Córdoba was established by Liñán (1978).

The Las Ermitas section Figure 1(C) belongs to the Pedroche Formation (300 metres). This formation consists of limestones and lutites, with occasional sandstone and dolostone intercalations Figure 1(D). This formation shows considerable lateral variations both in facies and thickness. The Pedroche Formation contains abundant archaeocyath build-ups, together with stromatolites, trilobites and a wide diversity of small shelly fossils (SSF). The fossil assemblages correspond to the Iberian Archaeocyath Zones I, II and III (*sensu* Perejón, 1984), indicating an early Ovetian age (Cambrian Series 2, Stage 3) (Liñán et al., 2004).

According to the original publication (Richter & Richter, 1927, p. 193), the holotype of. *I. carbonelli* was collected from an unspecified lutite level of the '*Archaeocyathus* formation' (nowadays Pedroche Formation) in the road slope next to the Las Ermitas fountain. Based on a schematic illustration by Rudolf Richter which was housed together with the specimen (see Supplementary Material 1), and on the comparison with the different lithologies along the section we tentatively locate the type strata of *I. carbonelli* at the second level of lutites with carbonate nodules of this section, as illustrated in Figure 1D.

Materials and methods

Photography and measurements

The type and only specimen (SMF X 696a) was collected by Rudolf and Emma Richter in the 1920s and is housed at the Senckenberg Museum of Frankfurt, Germany (SMF) (Supplementary Material 2). The specimen was photographed using a Nikon Z7 coupled with a macro lens Laowa 25 mm F2.8 2.5-5X Ultra Macro and an OGGLAB Vertical LED Lighting System. Measurements were made from photographs using ImageJ (Schneider et al., 2012), figures were constructed using Adobe Illustrator 2021 v. 25.2 and Inkscape 1.3.2 (https://www.inkscape.org).

Outline analysis

Black silhouettes on a white background of 17 species *Isoxys* species were taken from a previous study (Pates et al., 2021). Inkscape 1.3.2 was used to create a new silhouette for *Isoxys carbonelli* based off the type specimen and observations from this study. Silhouettes for sunellids *Combinivalvula chengjiangensis* Hou, 1987, *Sunella grandis* Huo, 1965 (morph A and morph B), and *Sunella* cf. *shensiella* Huo, 1965 (morph A and morph B), were created using reconstructions presented in Zhang and Shu (2007). The outline for '*Isoxys bispinatus*' (Cui in Huo et al., 1991) from Pates et al. (2021) was used for *Caudicaella bispinata* Cui and Huo, 1990, following the revision of this species by Sun et al. (2021).

Subsequent processing and analysis were conducted in R (R Core Team, 2024), using the *Momocs* package (Bonhomme et al., 2014), and code adapted from Pates et al. (2021). Silhouettes were converted into outlines using the *import_jpg* function, were scaled (*coo_scale*), centred (*coo_center*), and sampled (*coo_sample*) to the same number (64) of points, and then subjected to elliptical Fourier analysis (*efourier*). The *calibrate_harmonicpower_efourier* function was used to determine the number of harmonics that would capture 99.9% of the total harmonic power. Resulting harmonic coefficients were subjected to a principal components analysis

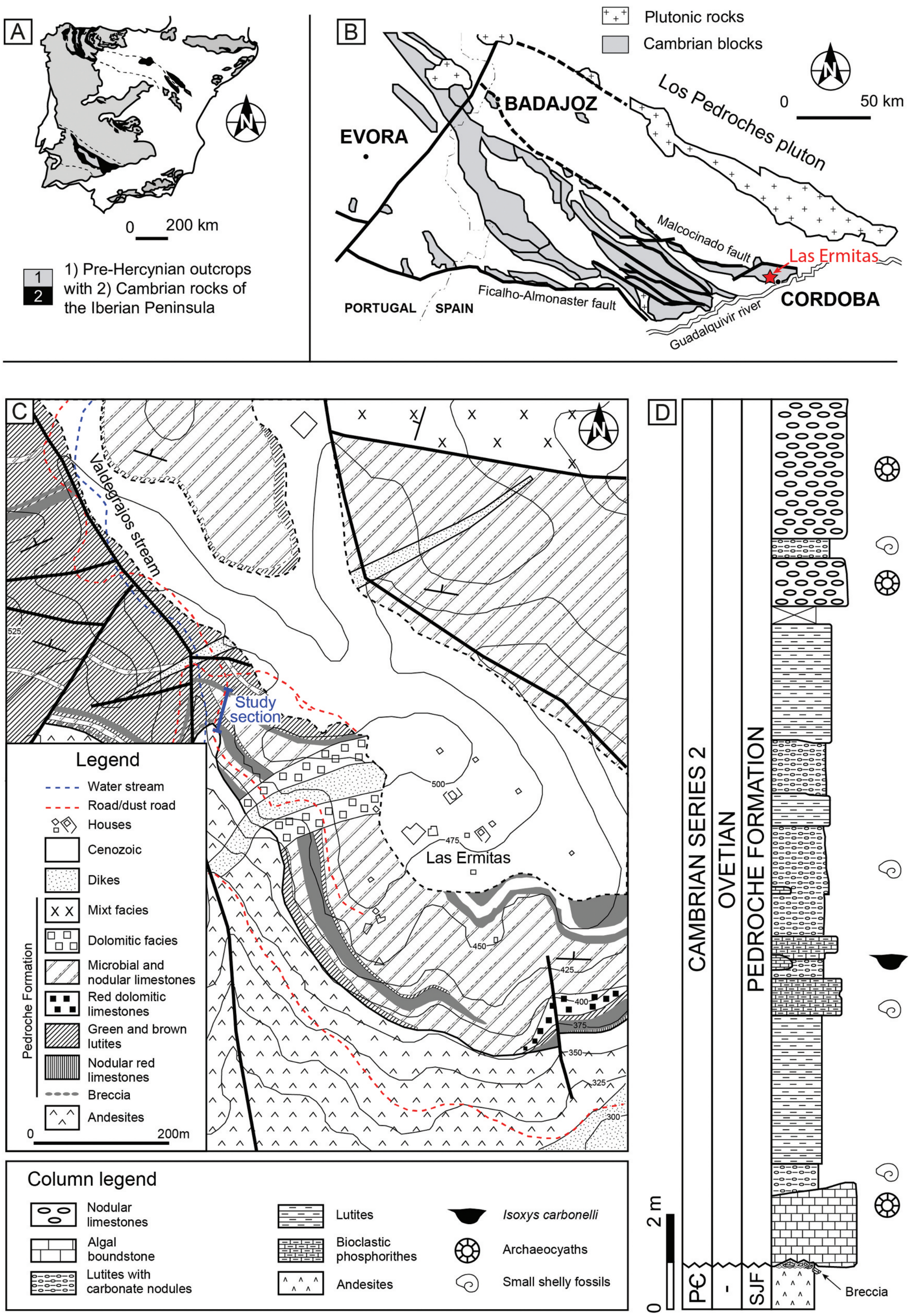

Figure 1. (A) Pre-hercynian outcrops in the Iberian Peninsula. (B) Simplified sketch-map of the main Cambrian outcrops of the Ossa-Morena Zone. (C) Detailed geological setting including the study section where *Isoxys carbonelli* was found, modified from Perejón and Moreno-Eiris (2007). (D) Stratigraphic column of Las Erminas section with the tentative location of *Isoxys carbonelli* within the Pedroche Formation, modified from Huang and Fernández-Remolar (2025).

(*PCA* function), which was used for visualisation. Hierarchical clustering analysis (*CLUST*) was applied to PCA results. Mathematical background and further details of elliptical Fourier analysis and the *Momocs* package are provided in Bonhomme et al. (2014).

Results

Isoxys carbonelli *morphology*

The type and only specimen measures 11.5 mm from the tip of the anterior spine ('as' in Figure 2) to the tip of the posterior spine ('ps' in Figure 2), and 4.5 mm at its maximum depth (distance between dorsal and ventral margins ['dm' and 'vm' in Figure 2], measured perpendicular to its long axis). The carapace outline is postplete, as the deepest part of the valve is just behind the midpoint of the carapace, 7 mm posterior to the anterior spine. The valve outline deflects with a posterior protrusion ('pp' in Figure 2) on the ventral-posterior margin. The anterior spine is longer (2 mm) than the posterior spine (<1 mm), though the blunt distal tips of both indicate that they may be incomplete. The carapace has a prominent cusp just behind the anterior spine ('cu' in Figure 2). No node is observed beneath the cusp. A faint line that runs from the anterodorsal region towards the anteromedial part of the valve is interpreted as a post-mortem wrinkle rather than an anterodorsal sulcus. Possible reticulations, visible as polygonal shapes around 0.5 mm in diameter, can be seen at the posterior of the valve ('re?' in Figure 2), towards the ventral margin. Faint evidence for a marginal rim ('mr' in Figure 2) can also be seen at this part of the valve.

Outline analysis

Seventeen harmonics were retained. Principal Component 1 (PC1) describes 65.6% of the variation, with PC2 12.1% and PC3 8.6%. PC4 describes 7.0%, with the remaining Principal Components describing less than 2.25%. Visualisation of PC1, PC2 and PC3 (Figure 3) reveals that PC1 describes the change from a slender carapace with long spines (positive PC1) to one with a greater depth:length ratio and short spines (negative PC1). Principal Component 2 describes a change from an asymmetric carapace with a prominent notch beneath the anterior cardinal spine and greatest valve depth anterior to the midline

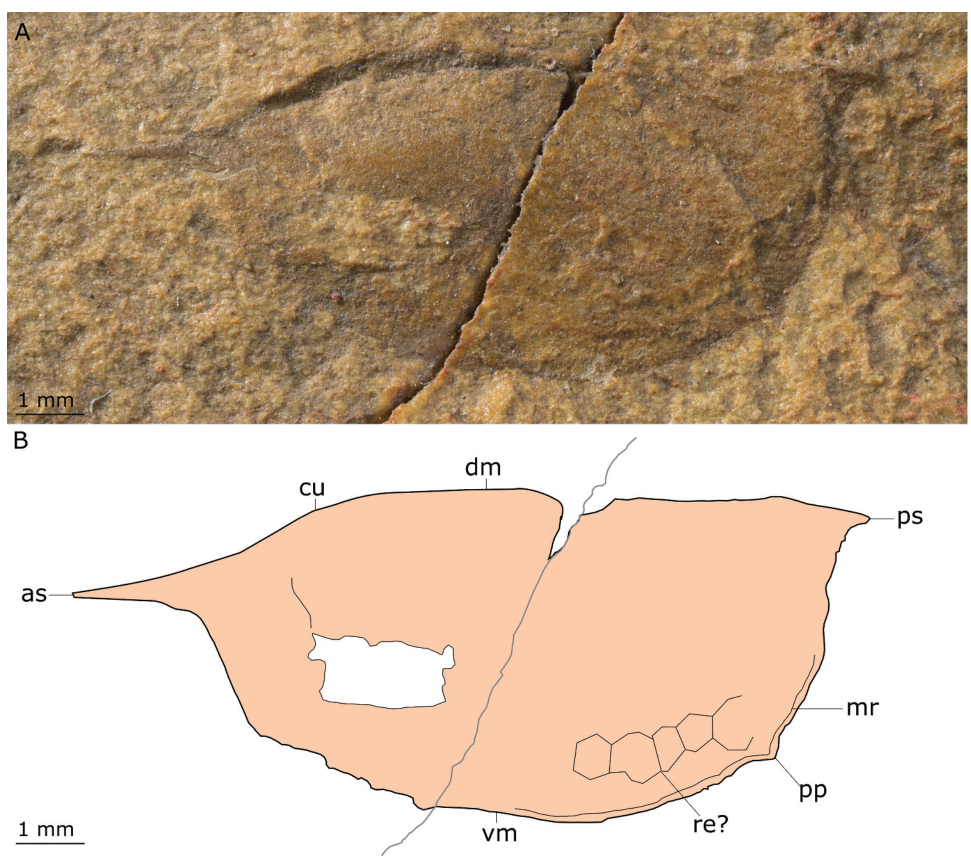

Figure 2. (A) Photograph and (B) line drawing showing anatomy of the holotype and only specimen of *Isoxys carbonelli* Richter & Richter, 1927 from the Ovetian (Cambrian Stage 3) Pedroche Formation, Spain. Abbreviations: as, anterior spine; cu, cusp; dm, dorsal margin; mr, margial rim; pp, posterior protrusion; ps, posterior spine; re, reticulation; vm, ventral margin.

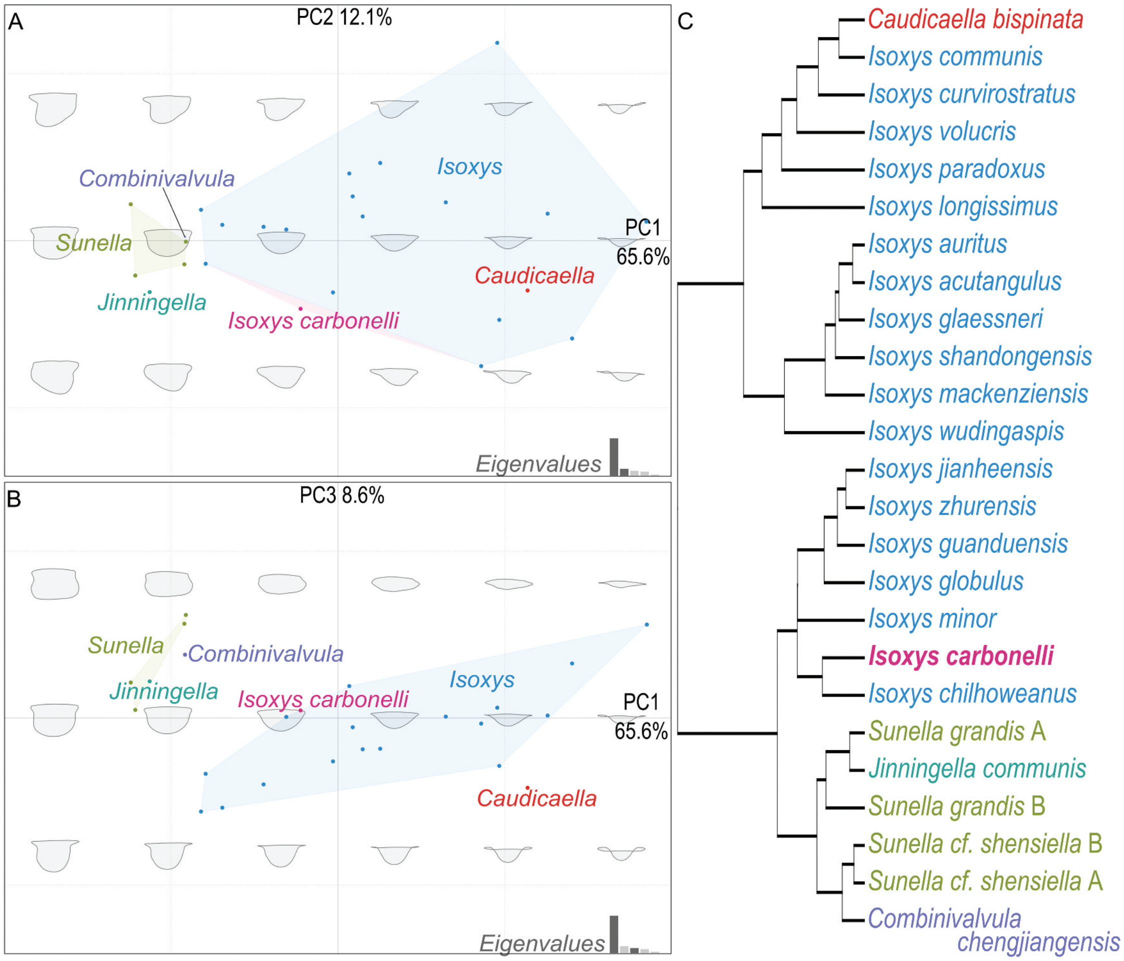

Figure 3. Results of the outline and cluster analyses comparing carapace outline shapes of *isoxys* species and sunellids. (A) Visualisation of principal components 1 and 2 on results of elliptical Fourier analysis. (B) Visualisation of principal components 1 and 3 on results of elliptical Fourier analysis. (C) Hierarchical cluster analysis on results of principal component analysis.

(positive PC2) to one with greatest valve depth posterior to the midline (negative PC2). The third principal component describes a change from a valve with approximately equal and nearly parallel dorsal and ventral margin lengths (positive PC3) to one with a much longer dorsal margin than ventral, and with a prominent curve on the ventral margin (negative PC3).

Isoxys and sunellids occupy distinct regions of the PC space. *Isoxys* taxa have higher PC1 scores, similar PC2 scores (but a broader range), and lower PC3 scores. *Caudicaella* Sun et al., 2021 occupies a very different position to other sunellids, with a very positive PC1 score, and negative PC2 and PC3 scores. *Isoxys carbonelli* falls within the range of other *Isoxys* PC1 and PC3 scores, occupying a position on the edge of the *Isoxys* convex hull in the space (Figure 3). *Isoxys carbonelli* has a higher PC1 score than any sunellid (except *Caudicaella*), and a slightly lower PC2 and PC3 score (again, except for *Caudicaella*).

These results are supported by the hierarchical clustering analysis. The first major division separates out the longer spined *Isoxys* and those with lower valve depth: length ratios (+ *Caudicaella*) from *Isoxys* with small spines and larger depth:length ratios. A further subdivision of each of these two large groups separates the longer spined *Isoxys* (+ *Caudicaella*) from those with shorter spines in the first group and separates the remaining sunellids from the *Isoxys* in the second group (Figure 3C). *Isoxys carbonelli* is recovered in the group of *Isoxys* sister to the sunellids, with a carapace outline shape most similar to the type species for the genus *Isoxys chilhoweanus* (Walcott, 1890).

Discussion

Comparison of Isoxys carbonelli *with sunellids and* Isoxys *species*

The recognition that sunellids were not restricted to South China but were also present in Gondwana during the Cambrian Stage 3 (Chen et al., 2025), alongside the recent reassignment of an *Isoxys* species to a sunellid (*Caudicaella bispinata* from the Cambrian Stage 3 Shuijingtuo Formation; see Sun et al., 2021), warrants comparisons of *Isoxys carbonelli* with sunellids. While the lack of soft parts in *I. carbonelli* precludes comparisons of the soft anatomy, where differences are clear (e.g. Zhang & Shu, 2007; Zhang et al., 2023), the carapace provides numerous characteristics for comparisons.

If the single known specimen represents an adult, *Isoxys carbonelli* would be the smallest *Isoxys* known at 11.5 mm, with most members of this genus reaching at least a few centimetres in length (e.g. García-Bellido, Paterson, et al., 2009). This species has a carapace length more similar to that of sunellids. *Caudicaella bispinata* (Shuijingtuo Formation), *C.* aff. *bispinata* (Heatherdale Formation) and *Sunella grandis* (Chengjiang biota) can reach over 15 mm, with most specimens of *Caudicaella bispinata* between 10 and 12 mm, and most *Sunella grandis* between 6.5 and 8.5 mm in length (Chen et al., 2025; Sun et al., 2021). *Caudicaella* aff. *bispinata* specimens are slightly larger than *C. bispinata* (Chen et al., 2025). Chengjiang sunellids *Combinivalvula* (Hou, 1987) and *Jinningella* also reached around 10 mm in length (Zhang & Shu, 2007, Figure 1). These sunellids have very short anterior and posterior spines (except for *Caudicaella bispinata*, where these spines are elongate), with those of *I. carbonelli* longer relative to the carapace length than *Combinivalvula, Jinningella* Huo & Shu, 1985 and *Sunella* Huo, 1965, but shorter than *Caudicaella* (Chen et al., 2025; Sun et al., 2021; Zhang & Shu, 2007). Reticulation is unknown in sunellids (Zhang & Shu, 2007), while all sunellids share a clear anterodorsal sulcus. Thus, the possible reticulation in *I. carbonelli* and lack of clear sulcus mark differences between sunellids and this taxon, alongside differences in carapace outline shape.

Notably, while *C. bispinata* does not cluster with the other sunellids, it also does not fall close to *I. carbonelli*. Instead, it is most similar to longer spined *Isoxys* and sister to *I. communis* in the cluster analysis.

Isoxys carbonelli has a higher carapace length:depth ratio (1.9:1, not including the length of the spines), than *Sunella grandis* (1.7:1; Sun et al., 2021), but this is very similar to *Caudicaella bispinata* (1.85:1; Sun et al., 2021). More broadly, the carapace outline of *I. carbonelli* is distinct from sunellids, with a greater asymmetry and more elongate spines (except *C. bispinata*) Figure 3(A, B), clustering with short-spined *Isoxys* taxa, most closely to *I. chilhoweanus*, the type species Figure 3(C).

The presence of a prominent anterodorsal cusp in *Isoxys carbonelli* is most reminiscent of the Sirius Passet taxon *I. volucris* Williams et al., 1996, though the spines of the latter are far more elongate and the carapace shape more symmetrical than *I. carbonelli*, and it has a much more prominent doublure (Stein et al., 2010). Smaller cusps relative to the carapace size are also known in the Emu Bay Shale taxon *I. communis* Glaessner, 1979 and Chengjiang taxon *I. curvirostratus* (Vannier & Chen, 2000), though these taxa again have longer spines, and their anterior spines have a dorsal curvature to them (e.g. Fu et al., 2011; García-Bellido, Paterson, et al., 2009). The short spines and general outline of the carapace of *I. carbonelli* is most similar to that of the Laurentian *I. chilhoweanus* and Australian *I. glaessneri* (García-Bellido, Paterson, et al., 2009; Walcott, 1890), with the latter also among the smaller *Isoxys* species and also from Gondwana, albeit known from a much higher latitude and Stage 4 rather than Stage 3. The posterior protrusion on the carapace outline present on the postero-ventral margin is unique amongst *Isoxys*, though some *Isoxys* species (e.g. *I. curvirostratus*) show a change in slope at this point, also observed in *I. carbonelli*.

In summary, *Isoxys carbonelli* shares more carapace characters with *Isoxys* species than sunellids, despite its small size (if it is an adult) being more similar to sunellids than *Isoxys*. This is supported by the outline analysis of carapace shape, and the more elongate spines relative to carapace size in *I. carbonelli* than sunellids (with the exception of *C. bispinata*).

Relative ages and palaeoenvironments of Isoxys *from the Cambrian Stage 3*

Isoxys had a broad geographic range already in the Cambrian Stage 3, with records from Laurentia, South China and Gondwana, albeit no records from high latitudes (Williams et al., 1996). *Isoxys* is well known from Cambrian Konservat Lagerstatten *sensu* Kimmig and Schiffbauer (2024) (e.g. García-Bellido, Paterson, et al., 2009; Williams et al., 1996), and is also known from some localities lacking in other non-biomineralized material, such as the Chilhowee Group (Tennessee, U.S.A.), Pedroche Formation (Córdoba, Spain), and Pestrotsvetnaya Formation (Siberia, Russia) (Ivantsov, 1990; Richter & Richter, 1927; Walcott, 1890). *Isoxys carbonelli* and *I. zhurensis* Ivantsov, 1990, from the latter two formations, are the oldest *Isoxys* taxa following the recent global correlation presented by Geyer (2019). These animals are found very soon after the first appearance of trilobites in their respective sequences (early Ovetian Stage and *Profallotaspis jakutensis* Biozone respectively; Gogin & Vdovets, 2013; Ivantsov, 1990;

Richter & Richter, 1927), close to the provisional base of Stage 3 and older than the Chengjiang biota (*Wutingaspis-Eoredlichia* Biozone) and Sirius Passet (*Nevadella* Biozone, upper Montezuman; Harper et al., 2019). *Isoxys chilhoweanus* (upper Montezuman; Webster & Hageman, 2018) is approximately coeval with taxa from these well-studied Stage 3 Lagerstätten.

While the paucity of data precludes extensive extrapolation from two data points, it is notable that the two earliest *Isoxys* species share a small size (<15 mm length, if they are adults), possessed short anterior and posterior spines, are both found in the bigotinid trilobite province, and lived in similar environments to one another, distinct from what is known from other Stage 3 *Isoxys*.

It seems that these earliest *Isoxys* lived in similar shallow, warm environments despite their distinct palaeocontinents (Gondwana and Siberia respectively). *Isoxys carbonelli* was found in levels associated with archaeocyaths and likely inhabited a reefal complex (Huang & Fernández-Remolar, 2025). *Isoxys zhurensis* was reported from a grey limestone in the Cape Zhurinskiy outcrop (Ivantsov, 1990), likely the stratotype section of the Atdabanian stage (Gogin & Vdovets, 2013). This section is associated with a reduction in sea level, with evaporite facies and shallow dolomite deposits indicating a shallow and warm environment including archaeocyaths (Gogin & Vdovets, 2013). These two earliest *Isoxys* taxa lived in a distinct environment to later *Isoxys* species, even from Stage 3. Other *Isoxys* from this time have been recovered from deposits representing a range of environments including the deltaic front of the Chengjiang (Saleh et al., 2022), the deeper Qingjiang (Fu et al., 2019; Ma et al., 2023) in South China, at the shelf-slope break below storm wave base in Sirius Passet (Harper et al., 2019; Nielsen et al., 2017) and outer shelf in the Chilhowee Group (Webster & Hageman, 2018).

Conclusions

The first detailed restudy of *Isoxys carbonelli* in nearly 100 years confirms that this taxon is still best considered an *Isoxys* species, rather than a sunellid, despite its small size. A posterior protrusion is identified on the carapace of this species for the first time, alongside possible reticulations and a thin marginal rim. The two oldest *Isoxys* species, *I. carbonelli* and *I. zhurensis*, both are known from similar shallow marine warm water carbonate environments in the bigotinid trilobite province, raising the possibility that *Isoxys* originated in this environment before spreading to a wide range of environments known later in the Cambrian.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data is uploaded to the Open Science Framework (DOI: 10.17605/OSF.IO/8WCZK). These data are photographs of the specimen, outlines used in the elliptical Fourier analysis, and R code required to run elliptical Fourier analysis, principal component analysis, and hierarchical clustering analysis.

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